

Horn growth in male pronghorns *Antilocapra americana*: selection for precocial maturation in stochastic environments

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Pronghorns *Antilocapra americana* (Ord, 1818), the sole member of a family unique to North America, grow rapidly and reproduce at an early age. Recent studies have found male pronghorns can grow large horns by 2 to 3 yrs of age. This pattern contrasts with many other ungulates, and it has profound implications for life history strategies. We examine 5 hypotheses that might explain precocial horn growth: (1) sampling bias, (2) nutrition, (3) phylogenetic inertia, (4) reproductive benefits conveyed by rapid horn growth alone, and (5) rapid horn growth as part of a suite of characteristics acquired due to precocial maturation. Hypotheses 1, 2 and 3 do not imply any natural selection, whereas hypotheses 4 and 5 do. We reject hypotheses 1, 2 and 4, and we cannot evaluate hypothesis 3. We conclude that hypothesis 5 most likely explains precocial maturation in male pronghorns, and mortality related to frequent, severe weather events may drive this pattern. We suggest several experiments to further examine relationships between age, size, and horn growth.

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Introduction

Life history theory predicts tradeoffs in allocating resources towards growth or reproduction (Stearns 1992). Ungulates often allocate energy toward growth at younger ages. Although males may produce viable sperm at 18–24 months, they typically delay reproduction until they reach maximum body and horn or antler size (Geist 1971, Clutton-Brock *et al.* 1982, Stewart *et al.* 2000, Festa-Bianchet *et al.* 2004). Furthermore,

in most ungulates, horn or antler size increases with age (Geist 1971, Bowyer 1986, McCorquodale *et al.* 1989, Bowyer *et al.* 2001).

Unlike most other ungulates, pronghorns *Antilocapra americana* (Ord, 1818) achieve maximum body size within 2 yrs (O’Gara 2004a). Previously, male pronghorns were thought to achieve maximum horn size at age 4 or 5 yrs (O’Gara 1990), but several studies across the species’ range documented a nonlinear relationship between horn length and age in male pronghorns, with males in all studies attaining

maximum horn size by 2 to 3 yrs of age (Menzel 1980, Min 1997, Mitchell and Maher 2001, Brown *et al.* 2003, O’Gara 2004a). Many bovids attain maximum body and horn size at the same time, but unlike pronghorns, most bovids continue to grow after age 2 (eg Geist 1971, Fandos and Vigal 1988, Pérez-Barbería *et al.* 1996, Clutton-Brock and Pemberton 2003). We consider 5 *a priori* hypotheses to explain this phenomenon of early horn growth in pronghorns: H1. Early horn growth is an artifact of sampling bias. Hunters selected for larger horned males of all ages in all populations. Natural selection plays no role in early horn growth; H2. Early horn growth is a function of population-specific nutrition. Males in populations with abundant, high quality forage grow larger horns than similarly aged males in other populations. Since variation is based on environmental differences, selection plays no role in early growth; H3. Early horn growth is a primitive condition retained from ancestral forms. Natural selection does not influence current early horn growth; H4. Early horn growth confers fitness benefits to male pronghorns. Thus, natural selection favors early horn growth, and H5. Early horn growth is part of the overall morphological pattern of early growth in pronghorns. Horns grow rapidly because, in general, pronghorns grow rapidly, and such horn growth incurs no significant energetic cost. Selection operates on a suite of characteristics, including early horn growth.

Methods

To evaluate the 5 hypotheses, we used studies of wild pronghorn populations located in Nebraska, Colorado, Montana, and New Mexico, USA (Menzel 1980, Min 1997, Mitchell and Maher 2001, Brown *et al.* 2003). In addition, we used previously published reports of pronghorn life history (reviewed in O’Gara 2004a, b, c, d).

Results

We reject H1 – sampling bias. All studies sampled pronghorns ranging from 1.5 to > 4 yrs, and Nebraska harvests included 50–60% yearling males (Menzel 1980). Whereas the proportion of young male pronghorns with large horns in the population may not be identical to that in the sample, young animals with small (24.8 cm) and large (42.9 cm) horns occurred in 3 of 4 populations examined (Menzel 1980, Min 1997, Mitchell and Maher 2001, Brown *et al.* 2003; Table 1). Therefore, the fact that 2- to 3-yr-old male pronghorns may, and at least sometimes do, grow large horns is unequivocal.

We also reject H2 – nutrition. Although the horn length-age curves differ, the same basic relationship occurred within and between different biomes with highly variable annual forage production (Mitchell and Maher 2001, Brown *et al.* 2003). Pronghorn age and horn size data sets considered in this paper were compiled from shortgrass prairie, semidesert grassland, and

Table 1. Mean \pm SE (range) of horn sizes (mean of left and right horns) in age classes of male pronghorns from Colorado, Montana, New Mexico and Nebraska. Nebraska data represent weighted means from 3 years of summarized data.

Population	Age class (years)							
	1.5	<i>n</i>	2.5	<i>n</i>	3.5	<i>n</i>	4.5	<i>n</i>
Colorado	17.3 \pm 0.7 (16.6 – 18.0)	2	30.7 \pm 0.8 (26.6 – 35.4)	11	32.1 \pm 1.3 (26.4 – 37.5)	8	33.8 \pm 0.8 (31.0 – 38.1)	9
Montana	21.3 \pm 2.7 (16.5 – 25.8)	3	32.9 \pm 0.6 (29.2 – 40.6)	20	33.6 \pm 0.6 (22.9 – 40.5)	32	33.8 \pm 0.4 (28.1 – 36.8)	30
New Mexico	–		39.3 \pm 0.9 (36.5 – 41.6)	6	39.1 \pm 0.8 (33.0 – 42.9)	15	38.3 \pm 0.2 (31.1 – 43.5)	117
Nebraska	18.7 \pm 0.2 (18.3 – 19.1)	309	30.3 \pm 0.6 (28.8 – 31.3)	241	34.1 \pm 0.1 (33.6 – 34.2)	119	34.3 \pm 0.7 (31.2 – 35.1)	118

shrub-steppe vegetation communities. In these plant communities, precipitation accurately predicts primary productivity, which in turn predicts standing crop biomass (Begon *et al.* 1990). Extreme variation in precipitation occurred within (< 159–225%) and between (9–1188%) study sites during the sampling periods (precipitation data from <http://www.wrcc.dri.edu/>), yet 2–3 yr old males grew horns as large as males 4 yrs and older under all conditions. Precipitation, primary productivity, forage quality, and subsequently nutrition may play a role in horn growth (Mitchell and Maher 2001), but the stage(s) of pronghorn life history at which these factors manifest themselves remains unclear.

We cannot evaluate H3 – phylogenetic inertia. We do not have access to sufficient fossil material to determine whether ancestral species exhibited the same patterns of age and horn size relationships as the sole remaining member of the taxon. We encourage other biologists to examine museum specimens of extinct Merycodontinae and Antilocaprinae for relationships between age, size, and horn growth patterns.

We reject H4 – fitness benefits of rapid horn growth alone. If males with larger horns reproduce more successfully, we would expect selection for large horns regardless of age. However, males with large horns do not necessarily achieve higher mating success or fitness (Byers *et al.* 1994). Although male displays toward females accentuate horn size, along with other secondary sexual characteristics (O’Gara 2004b), pronghorn females do not always select males with large horns as mates (Byers *et al.* 1994). Rather, females select males “...not for size or an irrelevant display feature, but for evidence of ability to sire vigorous offspring...” (Byers 1997).

We believe H5 – precocial maturation – best explains the observed data. Male pronghorns grow rapidly and become physiologically mature at 1.5–2 yrs of age (O’Gara 2004a). Although allometric equations differ phylogenetically, geographically, and taxonomically, horn or antler size correlates positively with body size or mass in many bovids and cervids (Bubenik 1990, Geist 1998), and horn size in male pronghorns increases with head size (Min 1997). Pronghorns also tend to be short-lived, with few males ex-

ceeding 9 yrs of age (O’Gara 2004a). Rapid physical growth, early sexual maturity, multiple mating strategies (O’Gara 2004b), and short life span all reflect selection for physical and behavioral attributes that contribute to successful competition for mates at an early age and increased lifetime reproductive success (Clutton-Brock 1988).

Discussion

Both male and female pronghorns exhibit rapid growth and maturation (O’Gara 2004a). Young of the year reach approximately 65% of adult size at 5 months, and males and females attain adult body size and mass by 18–24 months (Byers 1997). Females rarely breed as young as 5 months, and usually at 18 months, whereas males attain adult testes size and can breed at 18 months (O’Gara 2004d).

We propose that such precocial growth in pronghorns evolved in response to frequent weather-related mortality that targets older males. Life history theory predicts that mortality biased toward older age classes selects for early maturation and reproduction at younger ages (Charlesworth 1994). O’Gara (2004c) summarized > 10 studies documenting extensive pronghorn mortality (35–80%) in various areas across the species’ range. Weather-induced mortality frequently occurs (as often as every 5–10 yrs) due to summer droughts or heavy winter snowfall, and older males and young animals exhibit higher mortality rates during these weather-related events (Byers 1997, O’Gara 2004c, Byers *et al.* 2006). Periodic starvation is common in ungulate populations, but frequent mass mortality is rare (Clutton-Brock and Pemberton 2003). Rapid maturation allows pronghorns that survive frequent episodes of extensive weather-related mortality to successfully compete for mates and breed at early ages, which in turn allows for rapid population growth and recovery.

Bovid species inhabiting stochastic environments should display similar patterns as pronghorns, whereas species occupying more predictable habitats should exhibit longer maturation

times. Saiga (*Saiga tatarica* Linnaeus, 1766) and Soay sheep (*Ovis aries* Linnaeus, 1758) inhabit harsh, stochastic environments, experience similar frequent mortality events, and show similar life history responses as pronghorns, including mortality biased towards older males, precocial maturation of young, and attainment of adult horn size at early ages (Bekenov *et al.* 1998, Clutton-Brock and Pemberton 2003). Many mountain sheep and goats, on the other hand, inhabit more stable environments and continue to grow after sexual maturity, with horns increasing in size throughout their lives (Geist 1971, Schaller 1977). Early maturation allows adjustment to changing demographic and environmental conditions, thus contributing to successful reproduction.

We suggest several experiments to further test age and maturation relationships in pronghorns: (1) Collect true random samples for measurements. Document individual (ie size, mass, horn size) and population characteristics (ie densities, sex and age ratios) to determine if predictions are met for a given set of conditions; (2) Monitor male horn size over multiple years in one or more areas to determine if horn size changes predictably with changing environmental or social conditions; (3) Supplement pronghorn nutrition to determine if male horn size increases with improved nutrition; (4) Supplement female pronghorn nutrition to determine if neonate size increases with improved nutrition and if larger neonates grow larger as adults; (5) Quantify energetic costs of horn growth using captive pronghorns; (6) Experimentally manipulate horn size to determine if dominance or mating success changes accordingly, and (7) Measure growth and fitness in male pronghorns occupying habitats with greater and lesser degrees of stochasticity to test the prediction that more stochastic environments favor early maturation.

We agree with Gavin (1991) that understanding why animals behave as they do provides vital insights into population dynamics and processes. Examining horn growth in relation to other ecological and behavioral characteristics promotes a fuller understanding of the biology, ecology, behavior and evolution of this unique species.

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